An earth system approach to understanding the end Ordovician (Hirnantian) mass extinction

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ABSTRACT

The Hirnantian mass extinction (HME) is recognized as the first of the "Big Three," and along with the end- Permian and end- Cretaceous events results from an acceleration in biotic extinctions concomitant with a rise in originations. The HME is characterized by high taxonomic impact and within community extinctions. The HME is also unusual in that, a) it is associated with glaciation, but there is little evidence elsewhere in the younger Phanerozoic that glaciations have been a cause of mass extinction and, b) there is limited understanding of how glaciation directly causes mass extinction, particularly in the marine realm. In this review we argue coordinated extinctions occurred at the onset and termination of glaciation and, were due to climatically-induced changes in relative sea level, ocean redox stratification and sea surface temperature (SST) gradients. These earth system changes resulted in a reduction in prospective niche space both in the water column and on the seafloor, which in turn leadto increased competition and selection pressures leading to extinctions where the carrying capacities of particular ecological niches were exceeded. The long-term ventilation of the oceans broke the link between glaciation and mass extinction.

INTRODUCTION

The Hirnantian mass extinction (HME) is recognized as the first of the "Big Three," and along with the end- Permian and end- Cretaceous events results from an acceleration in biotic extinctions concomitant with a rise in originations (Bambach et al., 2004). Estimates indicate that in the marine realm 20% of families, 40% of genera (Sepkoski 1996) and by extrapolation about 85% of marine species went extinct at this time (Jablonski 1991) , making the HME second only in scale to the end-Permian in taxonomic impact. This extinction terminated the Great Ordovician Biodiversification Event (GOBE) and was followed by the Paleozoic plateau in biodiversity that continued until the end of the Paleozoic Era (Harper et al., 2013 in press).

Figure 1 about here

The HME is unusual in that, a) it is associated with glaciation, but there is little evidence elsewhere in the Phanerozoic that glaciations have been a cause of mass extinction and, b) there is limited understanding of how glaciation directly causes mass extinction, particularly in the marine realm. Pleistocene sea level changes did not much affect the marine biosphere at any ecological level (Valentine and Jablonski, 1991) and habitat tracking appears to have been an important process in insulating the biosphere from mass extinction at this time (Brett et al., 2007). Glacially-induced cooling, falling sea level and chemical recycling in the oceans are three of the many suggested kill mechanisms for end-Ordovician extinction, but a general consensus is lacking (Finnegan et al 2012; Harper et al., 2013 in press).

Figure 2 about here

The HME comprised two extinction phases which are known in some detail (e.g., (Brenchley and Cullen, 1984; Brenchley et al., 2006; Fig. 2). The "first strike", occurred at or just below, the *N. extraordinarius* graptolite biozone, and coincided with the onset of glaciation and a fall in global sea level (Fig. 3). Continental ice was centred on the supercontinent of Gondwana, located over the South Pole during the Late Ordovician (Brenchley and Cullen, 1984; Brenchley et al., 2001). During this phase, benthic organisms in deep and shallow-water environments were more affected than organisms occupying mid-shelfal depths. Planktonic/nektonic organisms, particularly graptolites, and nektonic groups, were differentially more greatly affected (Rasmussen and Harper, 2011a, b and references herein). The second strike, started at the base of the *N. persculptus* graptolite biozone, and coincided with a rise in sea-level and the widespread deposition of black shale in continental shelf settings (Fortey, 1989). During this phase coordinated extinctions occurred across the mid- outer shelf and particularly in mid-shelf settings.

Figure 3 about here

Global climate context

Estimates of the duration of the Hirnantian Glacial Maximum vary but may have been less than 1 myr (e.g. Armstrong, 2007; Holmden et al. 2012). A "short, sharp glaciation" cause for mass extinction can now be re-evaluated against a better understanding of longer-term Ordovician climate change and a large relatively new database of environmental proxies.

Figure 4 about here

Emerging new climate scenarios for the Ordovician indicate a modern "cool world" existed from the Early Ordovician (~472Ma; Trotter et al.,2008; Vandenbroucke et al., 2009) with successive glaciations during the Floian, Darriwilian, Katian (Guttenburg) and Hirnantian (Turner et al., 2011; Turner et al., 2012). These occurred against a backdrop of long-term declining pCO_2 (Godderis et al., 2001; Figs 4, 5) probably initiated by changes in plate configuration that resulted in increased weathering and nutrient cycling into the oceans, changes in volcanic outgassing of greenhouse gases and the re-direction of ocean currents. The rapid expansion of ice volume, during successive intervals of Ordovician glaciation was triggered by orbitally-induced cooling (Turner et al., 2011; Turner et al., 2012). During each glaciation the Gondwana ice sheet grew large enough to be affected by eccentricity-pacing of ice margin processes embedded in obliquity which largely controlled their size (Armstrong, 2007). Composite $\delta^{13}C_{carb}$ records for the entire Ordovician show a long-term broadly positive trend with increasingly large positive excursions through successive Ordovician glaciations (Bergström et al., 2009; Fig. 5).

Figure 5 about here

Positive isotope excursions (base Floian, DICE, GICE and HICE) coincide with intervals characterized by c. 1.2 myr long obliquity cycles, interpreted to indicate icehouse conditions (Boulila et al., 2011; Turner et al., 2011; Turner et al., 2012; Fig. 5). The $\delta^{13}C$ data suggest an ever-present Gondwana ice sheet that grew in a stepwise fashion to reach maximum size in the

Hirnantian. The Hirnantian Glaciation and associated mass extinction may thus be viewed as a "tipping point" in the Earth surface system, when the polar ice sheet was large enough to have a maximal effect on the ocean-atmosphere system (Armstrong, 2007).

Biotic patterns during mass extinction

Pattern 1. High taxonomic impact but low ecological impact.

No major taxonomic groups or trophic groups disappeared during the HME and the event has been classified as being of high taxonomic impact but low ecological impact (Droser et al., 2000; McGhee Jr et al., 2013). It is acknowledged that the Hirnantian biotic record is far from complete, largely documented at the level of geological stage and biased towards continental shelf settings in low paleo-latitudes. Despite this the patterns and trends of extinction are uneven across continents but these are as yet poorly documented and understood (Harper and Rong, 2008). Despite this the uneven pattern of extinctions likely provided refugia during peak glaciation as evidenced by a high proportion of Lazarus taxa (Brett et al., 2007; Rong et al., 2006). The relatively rapid recovery of the major clades and their benthic communities indicate minimal ecological disruption and largely within community species level extinction (Droser et al., 2000); this is particularly well-demonstrated by tropical communities. Despite significant global cooling, tropical bioherm communities remained largely unaffected by the HME and rugose and tabulate corals continued to radiate into the Silurian (Fig. 6A). Bioherms expanded rapidly during the Llandovery and went on to dominate many Silurian carbonate environments but, these communities had similar taxonomic compositions, species richness and trophic structure, to those of the Katian (Copper and Jin, 2012)

Figure 6 about here

Pattern 2. Variance in patterns of extinction between the benthic and pelagic realms.

The phytoplankton, including the acritarchs (chromophyte algae) and in deeper environments, cyanobacteria, formed the base of the food chain in Late Ordovician ecosystems. (Servais et al., 2008). Patterns of diversity decline are similar in phytoplankton, zooplankton and nektonic groups (Fig. 6B). All groups reach peak diversity in the late Darriwilian (Llandeilo) and show declining diversity through the Late Ordovician, recovering at a variety of rates until the mid- Silurian. The onset of diversity decline is significantly earlier than in benthic groups. Acritarch species-richness declined dramatically from the late Darriwilian (Llandeilo), with a similarly spectacular recovery in the Llandovery (Fig. 2, 6B). Chitinozoa and graptolites formed the preserved zooplankton and both groups declined markedly in diversity during the first strike of extinction. Graptolites were already in a state of decline from the Darriwilian (late Middle Ordovician); the group was reduced to only a few genera and less than 20 species by the first strike of the HME (Bapst et al., 2012). Graptolite disparity, as evidenced by a marked reduction in the range of graptolite rhabdosome and theca morphologies, also decreased during the mass extinction interval. However, many of the thecal morpho-types present in the Ordovician are found in the Silurian monograptids, suggesting these were hydrodynamic adaptations as the graptolites re-occupied specific niches (M. Williams pers comm., 2013) . Over 200 species have been reported from the Upper Llandovery (Lower Silurian; Zalasiewicz et al. 2009).

Species distribution studies indicate graptolites lived in two primary depth zones of the ocean waters. A shallow, epipelagic zone biotope contained species found preserved in all depth facies, whereas a deep, mesopelagic, zone biotope contained species now found only in deep-water facies (isograptid biofacies) (Cooper et al., 1991). Mesopelagic taxa thrived in continental-

139 margin upwelling zones and within the oxygen-minimum zone where their rhabdosomes were
140 preserved (Finney and Berry (1997). Epipelagic biotope species were affected by sea surface
141 temperature (see below). extinctions in the mesopelagic biotope are poorly constrained but
142 would have reflected oceanographic changes and feedbacks (especially upwelling and redox
143 conditions) that were driven by climatic and tectonic events (Finney and Berry 1997).
144 In the nekton, trilobites including the cyclopygids disappeared entirely. The top predators
145 of the Ordovician, the nautiloid cephalopods, were significantly reduced in diversity during the
146 extinction interval, from nearly 300 species at the height of the GOBE to some 50 during the
147 Hirnantian. This decline in diversity has been attributed to Early Hirnantian regression, draining
148 many of the epicontinental seas, and destroying habitats for potential prey (Harper et al., 2013 in
149 press).
150 In contrast, benthic groups, both sessile and motile, show diversity peaks at different times
151 (e.g. see papers in Webby et al. 2004) (Fig. 6A). Global analyses of Upper Ordovician and
152 Lower Silurian brachiopods indicate that 18.6% and 12.5% of families and 51.0% and 41.3% of
153 genera were eliminated in the first and second phases of the mass extinction, respectively, with
154 the total loss of 28.4% of families and 69.0% of genera in the crisis (Rong et al., 2006).
155 Although various major groups of brachiopods suffered substantially during the extinction, there
156 was clearly phylogenetic and ecological continuity between the Late Ordovician and Early
157 Silurian shelf faunas (Droser et al., 1997). The extinction of brachiopods did not cease at the
158 HME with a relict Ordovician association. Evidence from the Oslo Region and South China
159 suggests that part of the initial Silurian fauna consisted of the more eurytopic taxa of the
160 regressive succession that survived the extinction in the deeper parts of the intracratonic basin
161 (e.g. Baarli and Harper, 1986; Rong and Zhan, 2006; Owen et al. 2008). These species were

subsequently able to create and participate within new community structures during the Early Silurian transgression (Rong and Harper, 1999).

Through the HME trilobites suffered losses in the region of 70% at the generic level, and all unequivocally pelagic taxa became extinct by the end of the HME. Of the main trophic groups the filter feeders were differentially affected but did not disappear and these changes had little effect on the overall community structure (Adrain et al., 2004). In detail there is a marked, two-stage reduction in diversity at the base of the *N. extraordinarius* and *N. persculptus* graptolite biozones (Brenchley et al., 2001; see below). Benthic taxa that survived the first phase of extinction commonly succumbed to the second.

Pattern 3. Extinctions in the epipelagic zone were associated with a narrowing of temperature defined provinces

Figure 7 abut here

Biogeographical provinces are aggregations of communities and their number and individual compositions affect global or gamma biodiversity levels. Today temperature is the most important factor in defining the boundaries of biogeographical provinces that broadly follow the climate belts in the marine realm (Kucera 2007) . Paleobiogeographical studies of epipelagic organisms through the Late Ordovician indicate that during the Hirnantian Glaciation the latitudinal temperature gradient steepened and provinces shifted equator-wards (Vandenbroucke et al., 2010a; Vandenbroucke et al., 2010b; Fig. 7). These data suggest the geographical extent of the Tropical Province remained largely unaffected by the change from

inter-glaciation (Sandbian distribution) to Hirnantian glaciation. The low-diversity Polar Province expanded in geographical extent. Extinction was highest in the more diverse Subpolar Province, associated with the narrowing of the zone (Vandenbroucke et al., 2010a).

A link between species richness and provinciality is also recognized in brachiopods. Sheehan and Coorough (1990) recognised ten Katian brachiopod provinces, reduced to nine in the Hirnantian and only five in the Early to Middle Silurian. In contrast, Rong and Harper (1988) argued only three provinces could be recognized during the Hirnantian, the Edgewood, Kosov (broadly equivalent to the distribution of the typical *Hirnantia* Fauna) and Bani provinces; suggesting this difference in interpretation reflects the relative grouping of increasingly endemic faunas during the glaciation. Brachiopod diversity declines from the tropics into high latitudes (Harper and Mac Niocaill, 2002). In the early part of the Hirnantian the relatively low-diversity *Hirnantia* brachiopod fauna expanded towards the Equator (Temple, 1965), replacing the generally more diverse Edgewood Province that dominated the tropics (Harper, 1981; Rong, 1979). A similar pattern is reported with the widely-distributed *Mucronapsis* trilobite fauna (Owen, 1986).

Figure 8 about here

***Pattern 4. Benthic extinction was associated with depth*.**

Detailed analyses indicate the loss in alpha (within community; based on brachiopods) and beta (between community) biodiversity through the extinction events (Brenchley et al., 2001; Fig. 8). During the 1st strike percentage extinctions were high across the shelf but were higher in the outer shelf, Benthic Assemblage 6 (BA 6) characteristic of the outer shelf and upper slope

fauna (including the *Foliomena* brachiopod fauna), was completely eradicated. The second strike, further reduced diversity in the mid- and outer shelf biotas (BA 3 and 4/5), including the widespread cool water *Hirnantia* brachiopod fauna (Rong and Harper, 1988).

Geochemical evidence for changing ocean conditions during mass extinction

The Ordovician oceans were very different from those today (e.g., Munnecke et al., 2010). There is no direct evidence for the ventilation of the deep oceans. During the period anoxic ocean bottom waters were widespread and dissolved O_2 concentrations in the mixed layer are hypothesized to have been much reduced compared to the present day (Dahl et al., 2010); though this is difficult to reconcile with the presence of large, complex marine organisms and diverse multi-tiered communities. The fact that a large reservoir of anoxic deep water persisted below the storm and wave influenced mixed layer is corroborated by a number of geochemical and sedimentary proxies. Brenchley and Marshall (1999) argued that the positive $\delta^{13}C$ isotopic excursion during the Hirnantian, and now reported for earlier events in the Ordovician, could only be realistically sustained with the disposal of ^{12}C into anoxic deep oceans though this may be in part due to increased carbonate precipitation rates in eperic seas where high photosynthesis rates in biocalcifying bacteria, maintained by high nutrient fluxes, which locally increased the local carbonate-saturation state of the waters (LaPorte et al., 2009). Geochemical proxies, such as iron speciation, molybdenum concentrations and sulphur isotopes reveal complex patterns of changing regional and global redox conditions through the mass extinction (Figs. 9, 10).

Figure 9 about here

Figure 10 about here

Sedimentary evidence indicates oxygenated deposition at least at shelfal depths through the peak glaciation (*N. extraordinarius* graptolite biozone), for example there is a widespread shift from deposition of black shale to grey occasionally bioturbated, shale at specific localities (e.g. Dob's Linn; Armstrong and Coe, 1997). This is coincident with pyrite that is significantly enriched in ^{34}S in a number of sections (e.g. Goodfellow and Jonasson, 1984; Hammarlund et al., 2012; Zhang et al., 2009; Fig. 9). The last suggests a widespread reduction in marine sulphate concentrations that can be attributed to an increase in pyrite burial during the early Hirnantian. The ^{34}S-isotope excursion coincides with a major positive carbon isotope excursion recorded globally in marine carbonates (Fig. 9) and indicates increased photic zone photosynthetic productivity and organic carbon flux to the seafloor (Armstrong and Coe, 1997; Bergström et al., 2006; Brenchley et al., 1994; Finney et al., 1999; see also Kump et al., 1999). Together these proxies indicate that as global sea level fell, increased nutrient flux and photic zone bio-productivity intensified, widespread anoxic and in places euxinic conditions prevailed or expanded as the chemocline rose through the water column (Briggs et al., 1988; Fortey, 1989; Goodfellow and Jonasson, 1984; Zhang et al., 2009; though see Hammarlund et al., 2012 for an alternative view).

Rapid sea level fall can profoundly affect ocean chemistry, consistent with a pattern of increasing pyrite and organic carbon burial and a rising chemocline. As Hammarland et al (2012) observed as sea level falls, organic carbon produced by primary producers moves farther offshore and sinks through a deeper water column (Wallmann, 2003). The longer settling time of organic carbon leads to a more complete organic carbon decomposition and release and recycling of dissolved inorganic phosphate (DIP). Models show that a sea level drop of 100 m can result in

a more than 50% increase in marine DIP concentration, at steady state (Bjerrum et al., 2006; Wallmann, 2003). Consequently more phosphorus becomes available for primary production which in turn feeds back into increased organic matter production, oxygen consumption at depth and carbon burial. During a period of anoxic conditions, enhanced P regeneration from the sediment furthermore creates a positive feedback of P availability (Van Cappellen and Ingall, 1997). The last Pleistocene glaciation provides an analogue when deep ocean waters contained less oxygen than during the Holocene (de Boer et al., 2007; Sigman et al., 2004; Toggweiler and Russell, 2008).

Associated with these changes at depth an intensification of water column stratification would also steepen the oxygen gradient, reducing the habitable space for the plankton and nekton occupying the dysoxic zone (Berry et al., 1990; Fig. 11).

The *N. persculptus* Zone is characterized by a major sea level rise. Redox proxies from a limited number of sections suggest that anoxic, euxinic conditions and even ferruginous waters encroached onto the continental shelves (Hammarlund et al., 2012; Fig. 10). This change coincided with a declining productivity and carbon and pyrite burial, all complexly linked to declining ocean nutrient cycling during the post-glaciation period.

TOWARDS A UNIFIED EARTH SYSTEM MECHANISM OF GLACIALLY-INDUCED MASS EXTINCTION

Figure 11 about here

Figure 11 shows the results of a thought experiment, designed to explain the complex pattern of extinction within the benthos. The model shows the distribution of benthic assemblages from nearshore to offshore. Ecological boundaries within the water column, e.g. fair weather wave base, storm wave base and the chemocline are pinned at the boundaries of the benthic assemblages and maintain their depths during successive phases of the glaciation. This underlying aspect of the model can be tested using paleoecological and sedimentological evidence.

Brett et al. (1993) reviewed a variety of sedimentary and fossil evidence that could be used to estimate the absolute depth of the well-established depth gradient of Silurian onshore-to-offshore benthic assemblages (BA 1-5). This constrains much of the spectrum of benthic fossil communities to a narrow depth range, within the photic zone. They placed the depth of Silurian BA 1 through 4 to between 0 and 60 m. The absence of storm-disturbed beds over large parts of several major platforms below about the BA 3-4 boundary constrained the position of storm wave base. This is consistent with reports of Ordovician BA 4 through 6 being found in dysoxic waters below the storm wave base (Potter and Boucot, 1992). A more detailed study of the paleoecological controls of Ordovician benthic assemblages would provide an elegant test of the hypothesis.

Figure 11A shows the pre-glaciation template. During the first strike of extinction the expansion of the ice sheet resulted in a ~80m fall in global sea level (Loi et al., 2010) that is coincident with a rise in photosynthetic productivity and the chemocline rose through the water column. The complete extinction of taxa within BA 6 indicates the chemocline rose to shallow continental slope depths. The widths of the BA have been adjusted to maintain the depths of the ecological boundaries as described above. The result is to significantly reduce the widths of the

BAs compared to the pre-glaciation mode, particularly in BA 4-5. As shown in Figure 8 extinctions during first strike are found in all BAs but are preferentially higher in BA4-6.

During the second strike, rapid sea level rise to +100m (Brenchley et al., 1995b; see also Fig. 3) shifts the remaining BAs onshore and coincides with the rise of the chemocline onto the shelf and spread of anoxic/euxinic waters; supported by the redox proxy data. Again the widths of the BAs have been adjusted to maintain the constant depth of the ecological boundaries. The consequence is a further reduction in the widths of BA3 and BA 4-5, but significantly in BA3, a feature associated with higher percentage extinction in this benthic assemblage. The model predicts reduction in prospective niche space at the seafloor is the primary cause of diversity fall. Only BA6 is removed completely and community structures are maintained, though with reduced species richness.

DISCUSSION

Species go extinct for two main reasons: 1) population sizes are reduced to a point where chance events result in extinction or, 2) the niches species occupy disappear. Background extinction occurs all the time, but can these mechanisms be extrapolated to explain mass extinctions? At the current resolution of the available datasets it is difficult to test for reduced population sizes. The complex patterns of extinctions during the HME are set against a long term decline in global diversity, from at least the mid-Ordovician. The underlying cause of this decline is currently not understood and may reflect a reduction of ecospace as a response to the gradual cooling prior to the glacial maximum. Alternately, reduction in ecospace may have been provided by the destruction of terranes and microcontinents themselves. Detailed analyses of locality-based databases suggest that the diverse habitats of the island arcs of the Iapetus Ocean

were not sustained. This is particularly true for the peri-Laurentian terranes which were accreted to the Laurentian craton during the Appalachian–Caledonian orogeny. Terrane accretion was already underway prior to and during the Hirnantian (Rasmussen and Harper, 2011a).

The first strike of the HME has been attributed to cooling, reduced shelf areas as a result of sea-level drop, to globally increased ventilation of the oceans (Berry and Wilde, 1978; Brenchley et al., 1995a), expanding anoxia (Briggs et al., 1988; Fortey, 1989; Goodfellow and Jonasson, 1984; Hammarlund et al., 2012; Zhang et al., 2009) and the amalgamation of micro-continents (Rasmussen and Harper, 2011a). For the second strike, anoxia is widely considered the cause as indicated by the widespread deposition of black shale following a rise in sea level (Brenchley et al., 2001; Rasmussen and Harper, 2011a; Rong and Harper, 1988). These hypotheses largely fail to explicitly link the inferred mechanism to the recognized biological explanations for extinction.

We hypothesize that coordinated extinctions occurred as a consequence of climatically-induced changes in relative sea level, sea surface temperatures and ocean redox that resulted in the declining availability of prospective niche space in both pelagic/nektonic and benthic species (Fig. 12).

Figure 12 about here

This is a modification of the "shelf area hypothesis" which posits a relationship between species richness and habitable area, Phanerozoic species richness appears to have been in equilibrium with habitable area (Sepkoski, 1976). In the latest manifestation of this hypothesis Finnegan et al (2012) reported, based on sections from Laurentia, a link between tropical cooling and habitat loss. Sclafani and Holland (2013) also showed, using census data from Upper

Ordovician strata in Laurentia, a weak positive relationship between province area defined on geochemical parameters, and biodiversity though this was based on an untested assumption that Early Paleozoic communities were species saturated.

During the first phase of the HME, major eustatic sea-level fall removed significant habitable area on the continental shelves which lead to the down-shelf displacement of benthic assemblages, that coincided with a rise in the chemocline and an increase oxygen gradient reducing the habitable space for the plankton and nekton occupying the dysoxic zone in the oceans. Within the mixed layer declining diversity in planktonic provinces during the glacial maximum resulted from the steepening of latitudinal temperature gradients; which in turn resulted in the equator-ward spread of the low diversity Polar Province and the narrowing of high diversity provinces in the mid- latitudes.

During the eustatic sea level rise in the *persculptus* graptolite biozone, the potential increase of habitable shelf area was balanced by a narrowing of the shelf area occupied by BA 3 through 4/5 as ferruginous/euxinic water masses encroached onto the outer shelves, to close to storm wave base. During this interval the rise of the chemocline onto the shelves reduced habitable space coincident with a decline in diversity (Brenchley et al., 2001). The long-term ventilation of the oceans (Saltzman, 2005) and the deepening of the chemocline broke the link between glaciation and mass extinction.

A reduction in the area/volume occupied by a community either at the seafloor, within the water column or at the sea surface increased competition and selection pressures leading to extinctions where the carrying capacities of particular ecological niches were exceeded (Harper et al., 2013 in press; Saltzman, 2005; Sheehan, 1975, 2008; Valentine, 1969). In this way, within community extinctions are the predicted pattern of diversity change during the HME.

The availability of prospective niche space has implications not only for elevated extinction but post-extinction recovery. In the allopatric model of speciation, incipient new species arise continually as a consequence of gene mutation and allopatry. The constraint on the fixing of new species is the availability of expanding ecospace (Erwin, 2001). In this model recovery from the HME could not be initiated until ocean stratification and chemistry had returned to the pre-glacial equilibrium state..

CONCLUSIONS

- The HME coincided with the glacial maximum of the Early Palaeozoic Iceouse.
- Existing causative hypotheses fail to provide a biological context for the HME .
- We hypothesize that coordinated extinctions occurred as a consequence of glacially-induced changes in sea surface temperatures and ocean oxygen stratification that resulted in the declining availability of prospective niche space in both pelagic and benthic realms.
- During the first phase of the HME, major eustatic sea-level fall coincident with a rise in the chemocline and a steepening of the water column oxygen gradient, displaced benthic communities offshore into reduced habitable areas. Declining diversity in the plankton resulted from the steepening of latitudinal temperature gradients; resulting in the equator-ward spread of the low diversity Polar Province and the narrowing of high diversity provinces in the mid- latitudes.
- Following glacial termination, eustatic sea level rise in the *persculptus* graptolite biozone, a potential increase of habitable shelf area was balanced by a narrowing of the shelf area occupied by BA 3 through 4/5 as ferruginous/euxinic water masses encroached onto the outer shelves, to close to storm wave base.

- Together each phase of mass extinction can be related to a loss of habitable area and a reduction in prospective niche space. Elevated density dependent competition resulted in high levels of within community species extinction.
- HME was contingent on the unique nature of the Early Paleozoic oceans, with deep ocean anoxia. The effects of glaciations during the earlier Ordovician have yet to be studied in detail.
- The progressive ventilation of the oceans during the later Paleozoic and Mesozoic meant the biosphere would never again be subject to glacially-induced mass extinction.

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FIGURE CAPTIONS

Figure 1. Global biodiversity changes through the Phanerozoic. Family diversity of marine animals through the Phanerozoic indicating the three evolutionary faunas and microfossil record. The major extinction events (end Ordovician, late Devonian, end Permian, end Triassic and end

661 Cretaceous) are shown (after Sepkoski (1981). Solid arrows indicate mass extinctions where
662 extinction rates exceed small increases in originations; dashed arrows indicate mass extinctions
663 where reductions in origination exceed extinction.
664
665 Figure 2. Biotic change through the Hirnantian mass extinction. The brachiopod data indicate
666 the generic loss that appears to have been initiated already within the *pacificus* graptolite
667 biozone. After Brenchley et al., 2001 with modified brachiopod data from Rasmussen and
668 Harper, 2011b).
669
670 Figure 3. Late Ordovician-Early Silurian stratigraphy, stable isotope stratigrahy and relative sea
671 level change. The base of the Hirnantian is placed at the base of the *extraordinarius* graptoloite
672 biozone after Underwood et al., 1997). The carbon isotope profile is modified from Brenchley et
673 al., 1994 and the sea level curve is from Brenchley et al., 1995b). (Figure modified from
674 Brenchley et al., 2001).
675
676 Figure 4. Modelled atmospheric carbon dioxide and tropical sea surface temperatures through the
677 Cambrian to Silurian. Tropical sea surface temperatures are from Nardin et al. (2011), with the
678 grey area indicating the error envelope. Atmospheric carbon dioxide after Godderis et al., 2001).
679
680 Figure 5. Time stratigraphical diagram showing the chronostratigraphy and global composite
681 proxy data. (A, B) Data for relative sea level (after Haq and Schulter, 2008). (C) Stable carbon
682 (after Bergström et al., 2009). Grey horizontal boxes in B highlight the time periods of ~1.2 myr
683 cyclic changes in global sea level, interpreted as indicative of icehouse periods. GCIE is the

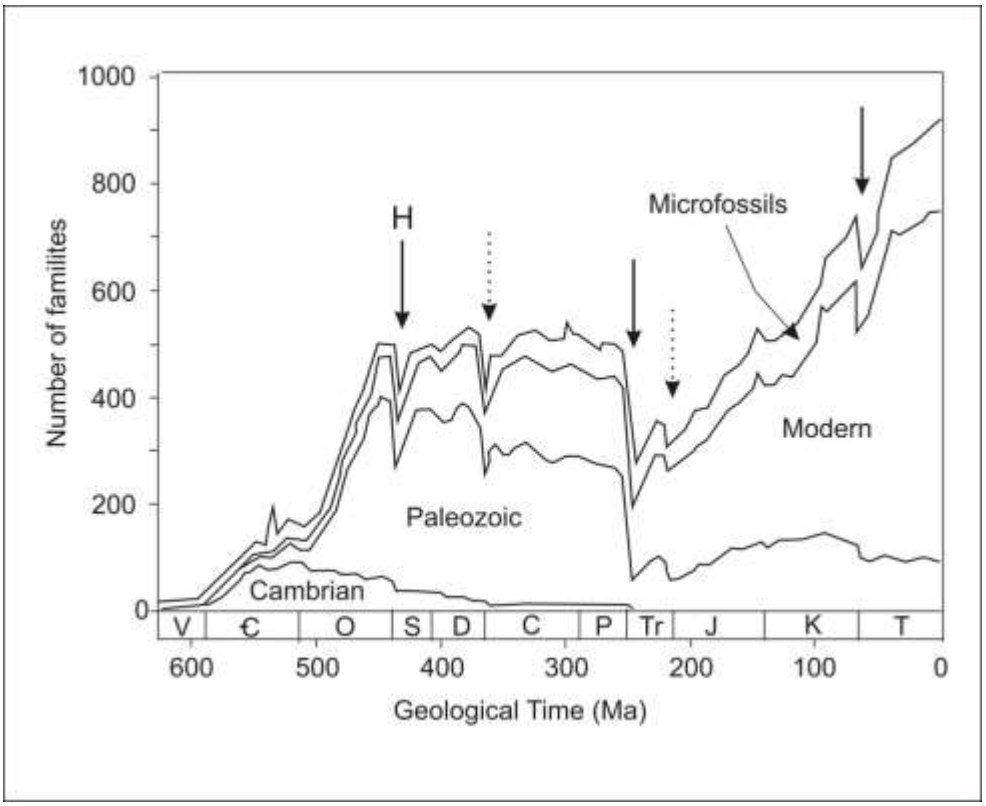
684 Guttenburg Carbon Isotope Excursion, HCIE is the Hirnantian Carbon Isotope Excursion. (After
685 Turner et al., 2011).
686
687 Figure 6. Biotic diversity during the Cambrian to Silurian. A. Benthic generic diversity. B.
688 Pelagic and nektonic taxonomic diversity. (Data from Sepkoski Online, downloaded March
689 2013). Note the data are assembled in the database using the British Series names. The Llanvirn
690 was extended by Fortey et al. (1995) to include part of the classical Llandeilo Series as a stage.
691 For convenience these are retained where appropriate in the text. British and globally recognised
692 divisions are compared in Figure 5.
693
694 Figure 7. Late Ordovician Polar Front migration. The figure compares the spatial distribution of
695 Sandbian, Hirnantian chitinozoan and graptolites and modern planktonic foraminiferan
696 provinces. The changing position of graptolite and chitinozoan provinces show an equator-ward
697 shift in the position of the Polar Front from 55° to 70° S to likely 40° S. This involves an
698 equator-ward incursion of Polar water and a narrowing of the Subpolar Province. The
699 Subtropical province moves slightly northwards. The migration of the Hirnantian Polar Front
700 compares well with known patterns from late Cenozoic interglacial to glacial transitions. (After
701 Vandenbroucke et al., 2010b).
702
703 Figure 8. Changes within brachiopod community (alpha) diversity across the continental shelf
704 and upper slope as calculated by Brenchley et al (2001). Numbers are an average taken from
705 communities within the benthic assemblage zones. There are no data for benthic assemblage 1.
706 Numbers in bold indicate the percentage decrease in mean alpha diversity at the first and second

strikes. The fall in alpha diversity after the first phase of extinction also includes the addition of new taxa belonging to the Hirnantian recovery fauna; no similar recovery fauna buffers the effect of the second phase of extinction. (Modified from Brenchley et al., 2001).

Figure 9. The Hirnantian mass extinction, glaciation and isotope excursions (from Hammarlund et al., 2012). A) Four major marine groups affected by the two-phased end Ordovician extinction, pre-, Hirnantian and post-Hirnantian refere to faunas (Brenchley et al., 1994). B) Interpolated $\delta^{18}O$ reflect fluctuations of Rawtheyan and Hirnantian sea level (Finnegan et al., 2011); LGM is the Last Glacial Maximum. C) Equatorial temperature fluctuations broadly parallel the $\delta^{18}O$ curve (Finnegan et al., 2011). D) A compilation of three profiles of inorganic $\delta^{13}C$ shows a significant perturbation of oceanic carbon cycle dynamics during the Hirnantian (Kump et al., 1999; LaPorte et al., 2009). E) A compilation of sulphur isotope data shows a major perturbation during the Hirnantian that parallels the $\delta^{13}C$ curve (Yan et al., 2009; Hammarlund et al., 2012).

Figure 10. Iron and molybdenum data for the sections at Dob's Linn, Scotland (GSSP for the base of the Silurian) and Billegrav, Denmark, reveal extensive euxinic, and occasional ferruginous, conditions. FeHR/FeT, highly reactive iron over total iron, has a threshold at 0.38. FePY/FeHR, the ratio of pyrite over highly reactive iron, filled circles are values above and open circles below 0.7. Mo, concentrations (ppm). The grey zone indicates the interval which is discussed as a lowermost threshold for euxinic conditions. (After Hammarlund et al., 2012).

729 Figure 11. Conceptual model illustrating the paleoenvironmental changes associated with
730 evolving sea level changes (rsl). Stars indicate the areas with greatest biodiversity decline. Fair
731 weather wave base (fwwb), storm wave base (swb) and pycnocline are fixed at the benthic
732 assemblage boundaries and maintain their depths during sea level change. The consequence is to
733 change the habitable area occupied by the benthic assemblages. Changes in habitable area are
734 consistent with areas of maximum species loss as shown in Figure 8.
735
736 Figure 12. Model showing the combined effects of oceanographical and climatic changes during
737 the mass extinction. Changing latitudinal temperature gradients affect the width and distribution
738 of the planktonic provinces (Polar, Subpolar, Tr, Transitional, Subtropical-Tropical).
739 Simultaneously, oceanographical changes associated with changing sea level and ocean redox
740 gradients affected benthic communities (f, fair weather wave base; s, storm wave base; c,
741 chemocline). The chemocline marks the top of anoxic deep ocean water. The combined effects
742 of both these processes was to reduce the habitable areas/prospective niche space and hence
743 increase competition between species leading to extinctions where the carrying capacities of
744 particular ecological niches were exceeded. Note there is are no continents on the North Pole to
745 support a major ice sheet.
746
747



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749 Figure 1

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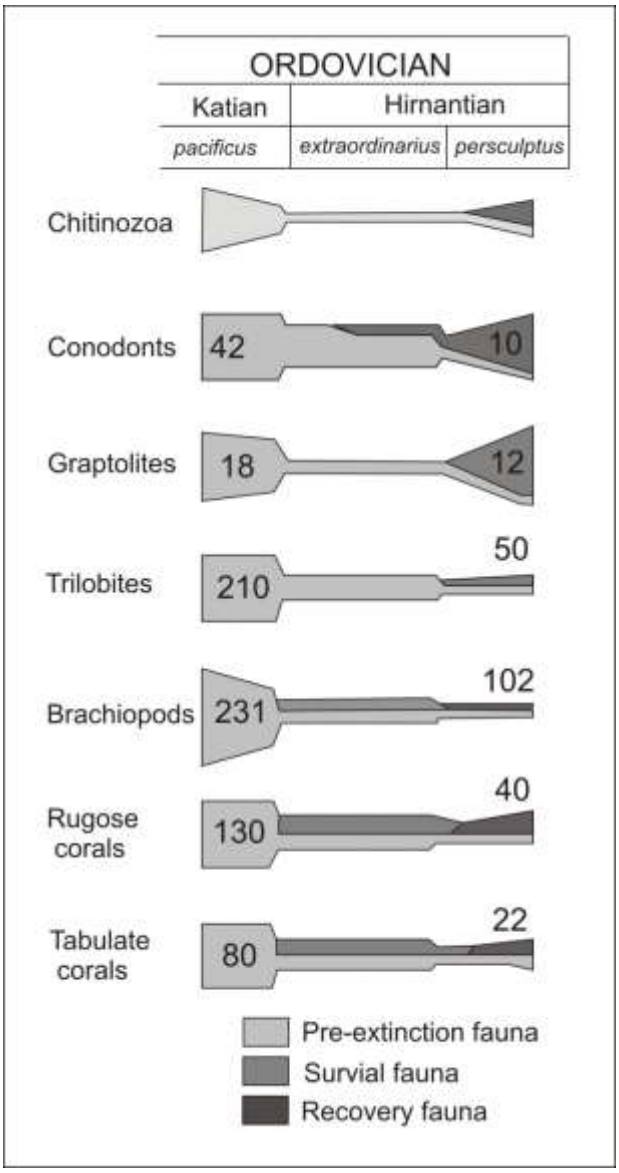

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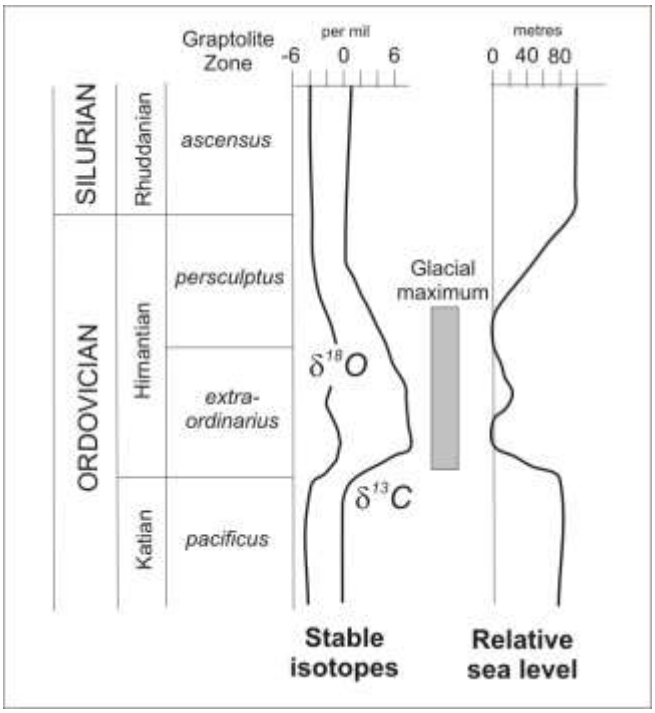
Graptolite Zone
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Stable isotopes
Relative sea level

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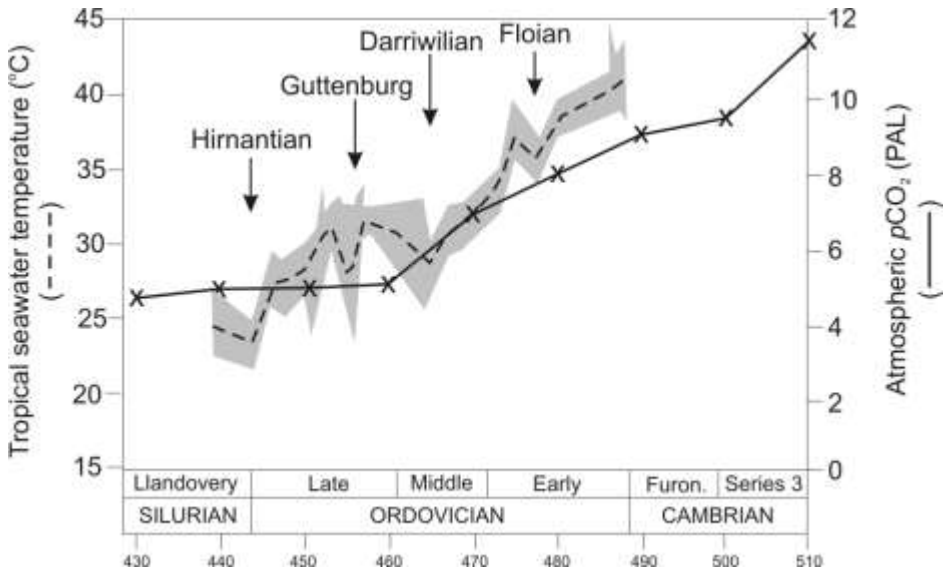

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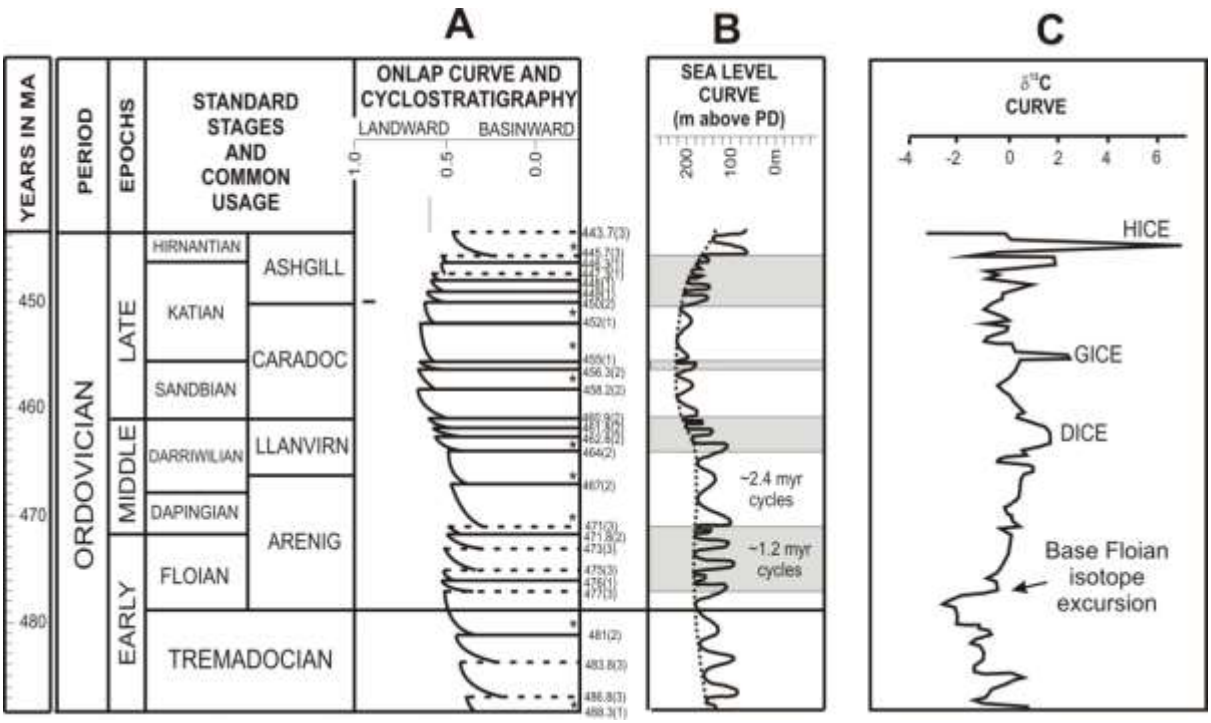

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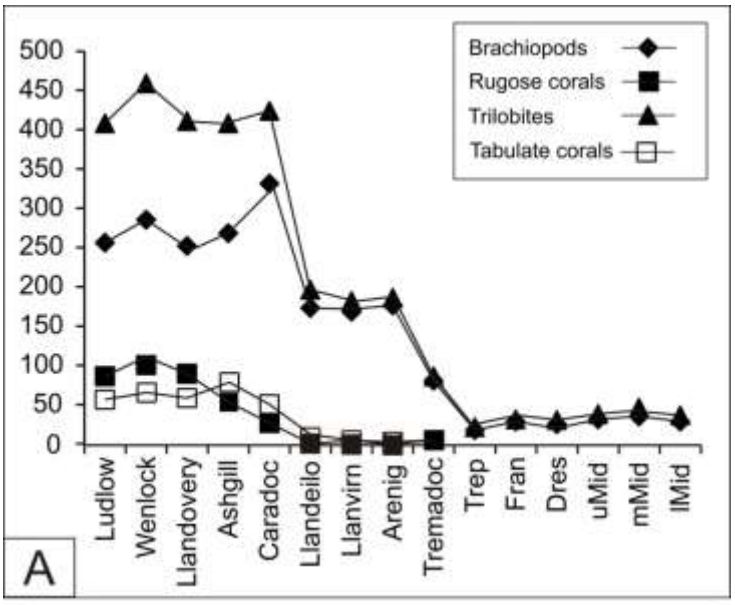

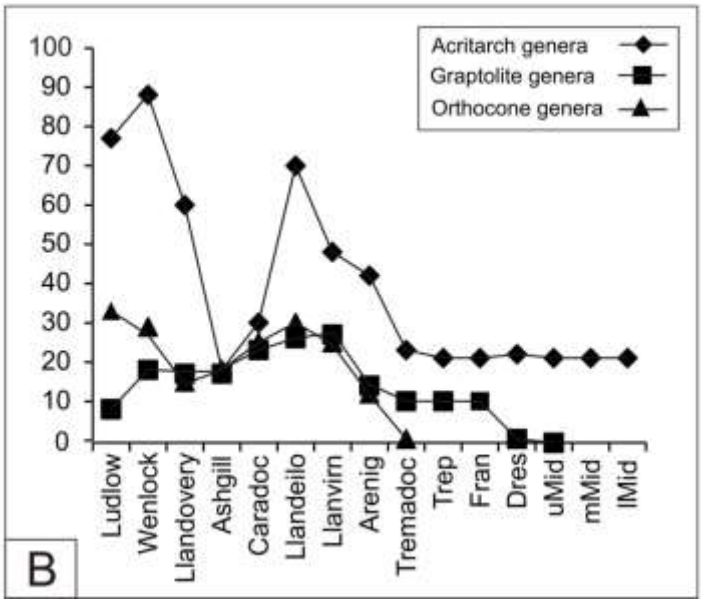

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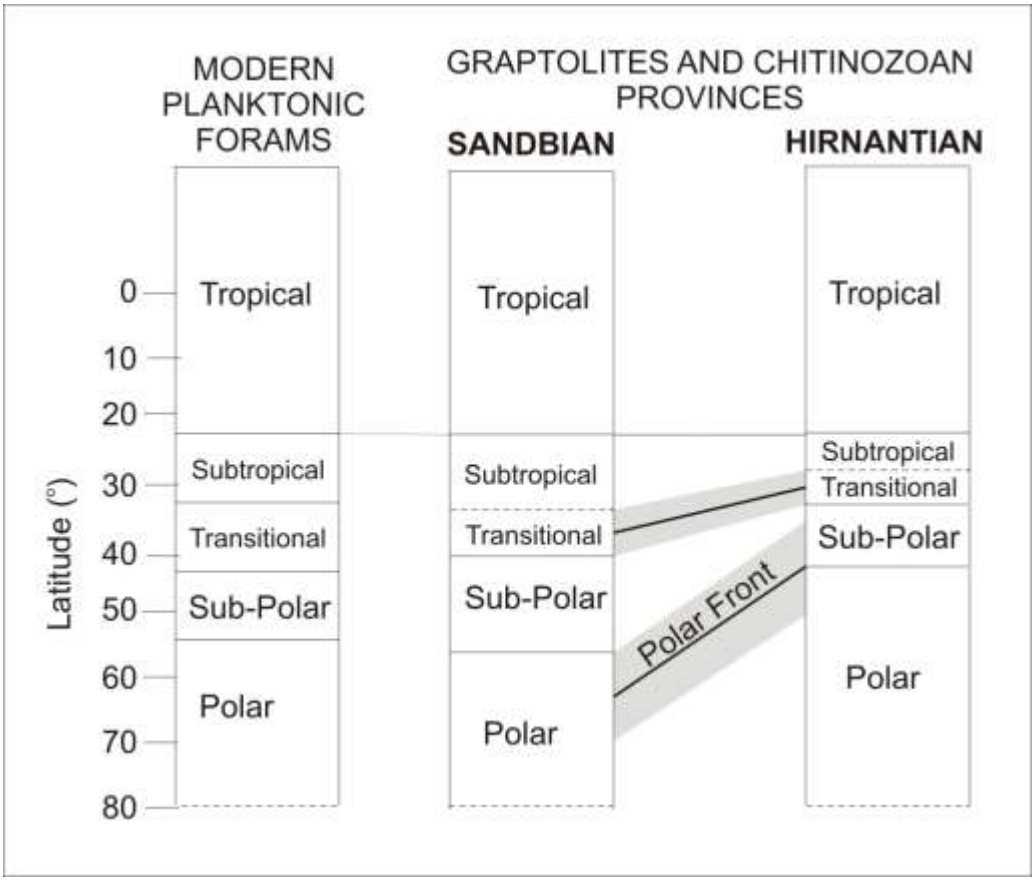
778 Figure 7



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781 Figure 8

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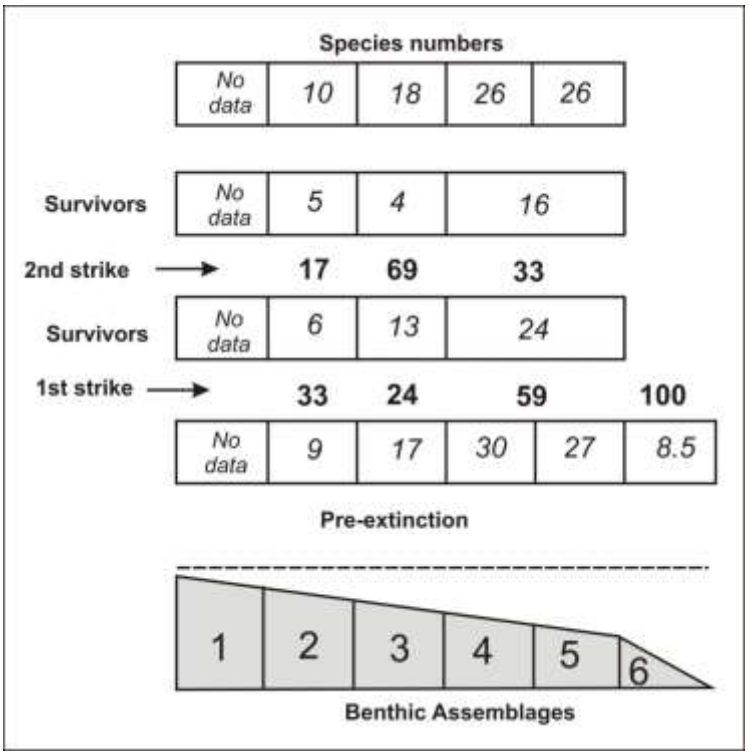

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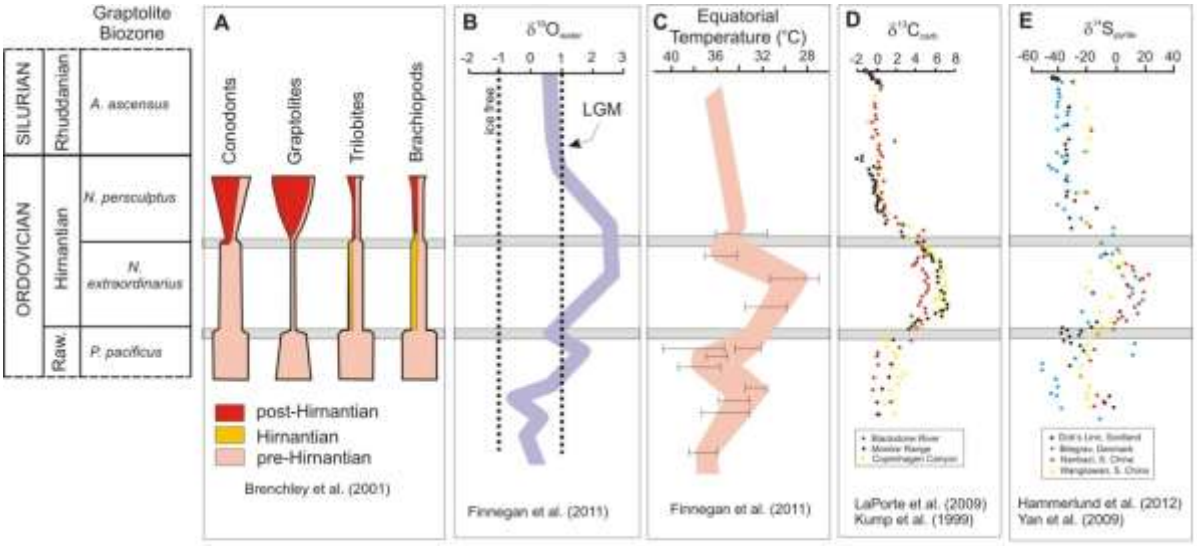
786 Figure 9



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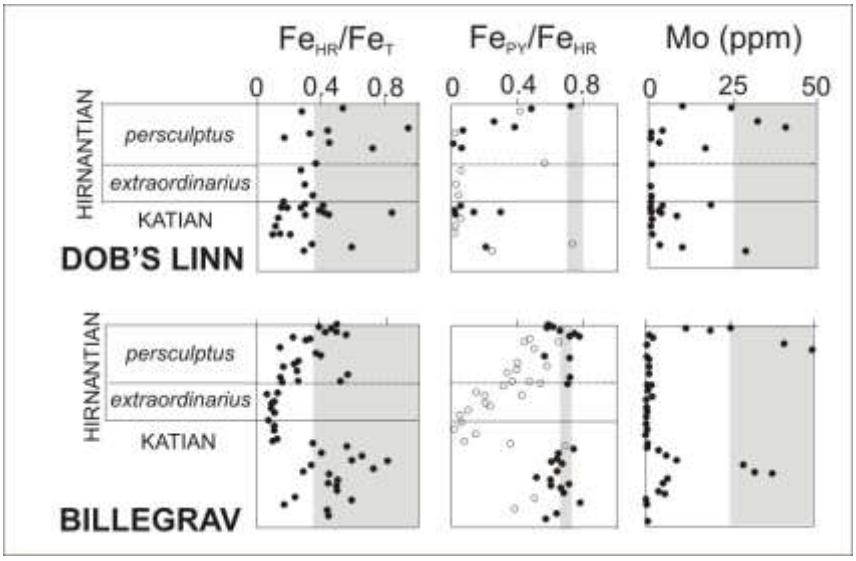
789 Figure 10.



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792 Figure 11

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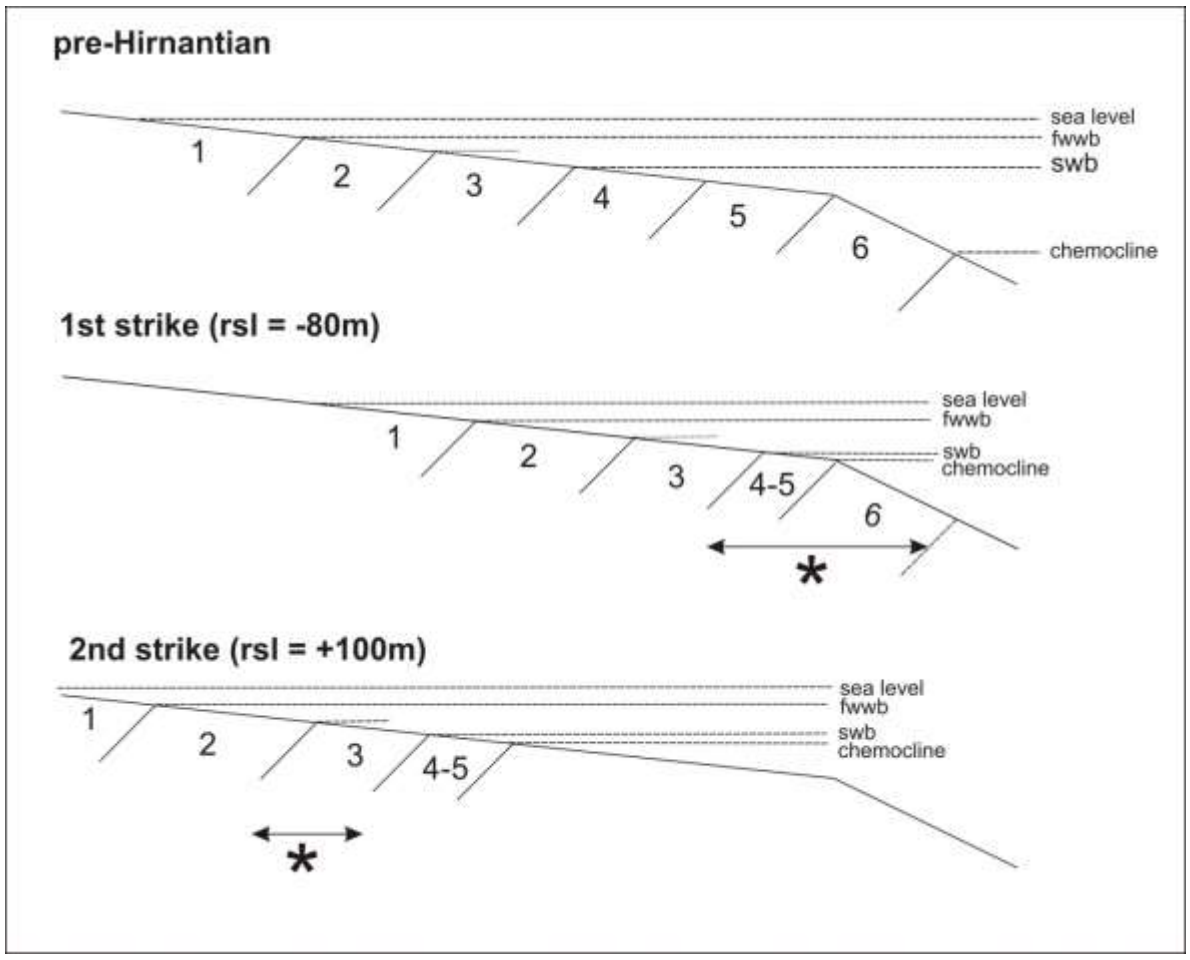

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797 Figure 12

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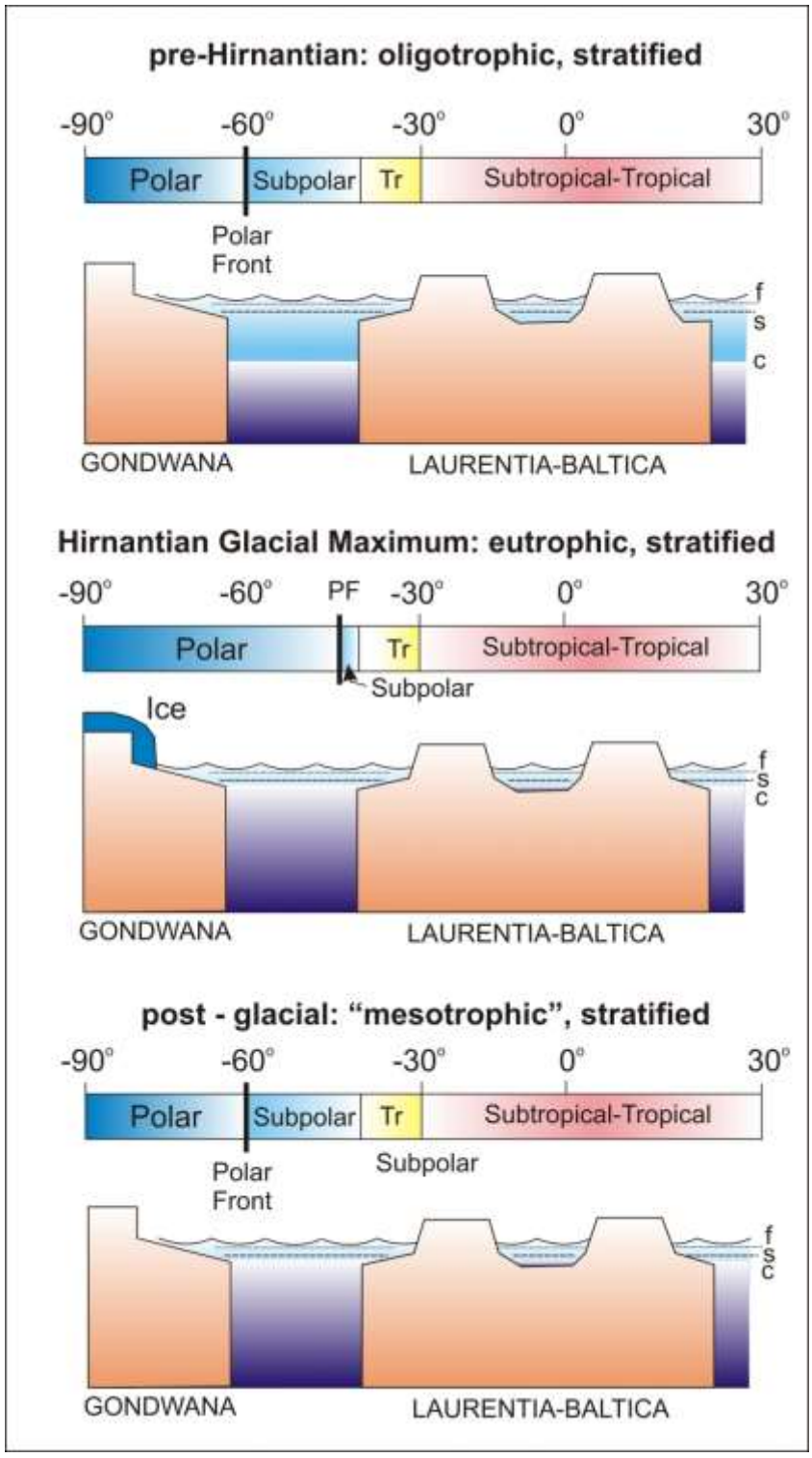

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